THE ROLE OF SOME HALORAGACEAE IN ALGAL ECOLOGY

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While collecting vascular aquatic plants in several ponds in east-central Massachusetts we found that there was a considerable accumulation of algae upon some of the vascular species, but very little on others. The present paper is the result of our futher observations on and examination of the relationship between the algae and the vascular plants upon whose surfaces they were found.

There is little published data elaborating the substrate preferences of fresh-water algae. Water chemistry, light, temperature, water density, pH, and a wide variety of metabolic processes have been treated frequently (see Jackson, 1964, and Smith, 1950) as environmental factors in algal growth. Reference texts (e.g., Prescott, 1962) indicate that some species of algae are epilithic, endophytic, or epizooic, or that many are epiphytic upon vascular plants or larger algae. Other than Chapman (1962) there seems to be no treatment of situations in which the algae have the opportunity to grow on or in association with a variety of substrates and in which clearly some means of preference for one another is established. Tiffany (1951), for example, suggested that the amount of substrate available to the spores for fixation is of major importance to algal growth, but he fails to include any discussion of the character of the substrate itself, or of the various environmental factors that might be operative in the selection and utilization of a particular substrate. Chapman suggests that, (1) the age and nature of the substrate flora are important, (2) diatoms are more likely to be on older leaves, (3) epiphytes are most numerous on well lighted surfaces, (4) epiphytes are most numerous on submerged material, (5) depressions between cells of the host surface seem to provide better substrate for attachment, and (6) ponds with muddy bottoms have a reduced number of epiphytes. With few epiphytes occurring in our collections we tend to agree with the last premise, but we have insufficient evidence to either support or refute the other ideas. We might generally suggest, however, that rather similar principles may operate for both tychoplankters and epiphytes.

Our examination of material from different ponds clearly showed that algae grew profusely upon some vascular plants but sparsely or rarely on others. We also found that both the number of species and the types of tychoplankter algae varied with similar plants in different environments. In order to identify, if possible, the operative environmental factors, we selected two sites in which the algal habitats might be contrasted. In both instances, (1) a small leaved aquatic plant was the primary algal substrate, (2) the substrate plant grew in the shallower portions of the pond, (3) both ponds and collecting sites were in virtually identical locations beside highways, and (4) there was no shading of the collecting stations by macrovegetation on or near the banks of the pond.

THE POND STATIONS

1. Pratt Pond. This pond is located at the junction of Grove Street, Hopkinton Road, and Westboro Road in the town of Upton, Worcester County, Massachusetts.

All collections were made in the western sector of Pratt, from water varying between 1.5 and 2.0 meters in depth. Most of the remainder of the pond is sufficiently deep so as to permit swimming and diving. The bottom of the pond is sandy-mud throughout. The pH averaged 6.5 and the alkalinity was 3 ppm.

The dominant vascular aquatic in the collection area of Pratt was *Myriophyllum heterophyllum* Michx., occurring over more than one-third of the center of the bay. In so far as we were able to determine during the several months of field work, no other vascular plant grew in or near the stand of *Myriophyllum*. This resulted in a clear zone around the stand extending to within several meters of the pond's edge.

In this shallower water a few other rooted aquatics grew sparsely. Of these *Nymphaea odorata* Ait., *Pontederia cordata* L., and *Potamogeton spirillus* Tuckerm., were the most common.

2. Icehouse Pond. This pond is beside West Main Street, 0.9 kilometers east of Interstate Route 495, in the town of Hopkinton, Middlesex County, Massachusetts.

Samples were collected from water up to 0.5 meters in depth along the southern edge of the pond. The deepest portion of this pond was approximately 1.5 meters, the bottom being mud and gravel. Water loss from this pond during the late summer months left some of the westerly edges as exposed mud and rocks. The pH averaged 6.1, and the alkalinity was 3.5 ppm.

The shallow waters of this pond were densely populated with a variety of rooted aquatic plants. Algae were associated most profusely with *Proserpinaca palustris* L., which grew in scattered stands of a few plants each. Other common vascular plants in the collection area were *Potamogeton pulcher* Tuckerm., *P. capillaceus* Poir., *Eleocharis acicularis* (L.) R. & S., *Pontederia cordata* f. *taenia* Fassett, *Nymphaea odorata* Ait., *Nuphar variegatum* Engelm., *Brasenia schreberi* Gmel., *Ludwigia palustris* var. *americana* (DC.) Fern. & Grisc., *Callitriche verna* L., *Myriophyllum humile* (Raf.) Morong, and *Utricularia purpurea* Walt.

PROCEDURE

Samples of the vascular plants were collected from the two pond stations and the species determination made using Fassett (1966) and Fernald (1950). Representative specimens were pressed and are in the herbarium at Boston State College.

Samples of the primary substrate plants were collected, some portions retained fresh for immediate scrutiny, and the remainder preserved in a solution of 3% formalin. Determination of the associated algal species was made from Smith (1924), Irenee-Marie (1939), Prescott (1964), and Patrick & Reimer (1966). Microscope slides were made of some algae using the Kaiser Glycerin-Gelatin method in order to facilitate drawing by camera lucida. All other samples were placed in Transeau's Fluid for permanent storage.

DISCUSSION

Twenty-one species of algae were found on or in association with *Myriophyllum heterophyllum* in Pratt Pond. Sixty-one algal taxa were discovered in various degrees of association with *Proserpinaca palustris* in Icehouse Pond. Seven species were common to each pond. The wide disparity in numbers despite virtually simultaneous collection times strongly suggests that *Proserpinaca* offers a more favorable habitat to the algae than does *Myriophyllum*. Inasmuch as a difference in surface characteristics might lead to the difference in habitats, it was the first possibility examined. We were not able to substantiate such a premise on any physical basis. One of the problems, however, is that only five genera of epiphytes were recorded during the study. *Stigeoclonium* and *Characium* each had one species present infrequently in Pratt Pond, while *Bulbochaete* and *Gloeotrichia* each had one commonly found species in Icehouse Pond, and *Oedogonium* with one common species and one infrequently encountered, both in Icehouse Pond. The pattern of occurrence of these was generally the same as for the tychoplankters and appeared to be due to the overall differences in the habitats rather than individual differences between the substrate plants.

Thus it seemed likely that there was a combination of factors operating in each situation, with sufficient variance between the two habitats such as to account for the difference in algal populations. This view is strengthened by the difference in tychoplankter populations, Icehouse Pond having approximately twice as many taxa. Inasmuch as the tychoplankters do not adhere to a particular substrate, but live in association with the substrate, they would not necessarily be affected by physical characteristics.

Some previous work gave direction to our scrutiny. Anderson & Walker (1920) concluded from an investigation of some shallow Nebraska lakes that light and mechanical support are of primary influence to algal growth. They also suggested that shallow water and wind protection give rise to as nearly uniform conditions as possible. Needham & Lloyd (1916) showed that in shallow waters with abundant vegetation currents are reduced or eliminated and there is little possibility of wind disturbance. The authors' own experience has been that tychoplankter populations are particularly rich among the wet sphagnum of New England bogs.

Comparison of the two sites on these bases yielded some rather interesting results. It has already been stated that sunlight was readily and equally available to the water in which both sets of substrate plants grew. The collecting area in Icehouse Pond, however, was much shallower than that of Pratt Pond. This difference was negated by the position of the tychoplankter algae in Pratt Pond; they were all within ½ meter of the surface of the water. The only living algae below that level in Pratt Pond were diatoms, and they were usually obscured by the detritus on the lower branches of plants of *Myriophyllum*.

Physically, Icehouse Pond is protected from surface winds by the mixed deciduous-coniferous forest around it. Although its total surface area approximates that of the section of Pratt Pond from which we collected, we were unable to observe more than mere surface ripples on Icehouse Pond during any visit to the site. Part of the reason for this is the dense vegetation within the water itself. At Pratt Pond, however, we were able to note considerable surface disturbance by even relatively light wind currents.

We were unable to observe any current within Icehouse Pond. This is largely due to the dense aquatic vegetation. Water movement could easily be discerned in Pratt Pond. As we collected samples in Pratt Pond, broken pieces of *Myriophyllum* would rise within the stand of plants then drift "downwind." Our observation of this phenomenon showed that the drag of the wind on the surface of the water caused the upper portion of the water to move, creating an effective pull on the lower water body. Water then rose through the plants and downwind. Davis (1955) suggested that tychoplankters would be unable to adapt evolutionarily to such current conditions. On the basis of our limited work we concur, finding no evidence of specialized attachment structures or polymorphism which would give any species an advantage in maintaining its position. It appears to us that the lack of water movement within Icehouse Pond is conducive to an optimum interchange of chemical nutrients. On the other hand, the flow within Pratt Pond apparently reduces a similar interchange, thus inhibiting population growth to some degree.

Our final consideration was the growth habit of the small leaved algal substrates and the associated macroflora. In Pratt Pond *Myriophyllum* produced vertical axes greater than the depth of the water. Near the surface of the water the distal portions of the plants would bend with the drag of the surface water. This appeared to produce a matting effect at the surface which would effectively reduce the light available to lower levels. The *Proserpinaca* in Icehouse Pond grew only to the surface of the water and distal flexing was rare and then of a minor nature. Light could pass easily through the finely dissected leaves to lower levels. Moreover, the densely crowded vegetation of Icehouse Pond effectively reduced lateral "waving" by the plant. *Proserpinaca* occurred in larger clumps than any of the other small leaved plants in Icehouse Pond (e.g., *Myriophyllum, Utricularia*).

Examination of the broader-leaved aquatics in each pond did not reveal any substantial amount of algae growing on or associated with them. The most frequent species were diatoms, *Tabellaria,* for example, being the most common.

SUMMARY

From our observations we conclude that for the optimum growth of tychoplankter algae there are at least three basic requirements. Not necessarily in order of importance they

are: (1) a substrate which provides both maximum surface area and exposure to the available light; (2) an absence of strong or prolonged water currents; and (3) the presence of a varied flora which provides a broad spectrum of nutrients within the system.

Based on our observations at both ponds we suggest that small leaved plants will most often provide the optimum habitat for tychoplankter algae. We are not convinced, however, that monospecific stands provide the optimum environment for tychoplankters, although such stands may be the best of the available substrates. We have found comparable situations in bogs, as it has been our experience that the sphagnum bogs with the greatest variety of macroflora usually yield the largest number of algal species.

We further suggest that pH and water temperatures are primarily useful only in contrasting regions with geographical and/or geological differences. It can be reasonably inferred that evolution has already adapted local algal species to pH and water temperature as they occur in the algal habitat.

Finally, we concur with previous workers who have suggested that quiet, stable and uniform water conditions are best for the growth of tychoplankter algal populations.

The list of algae below follows the sequence of Smith (1950). Nomenclature of the Bacillariophyceae is according to Patrick & Reimer (1966). Location and frequency are indicated by the following: IP — Icehouse Pond, PP — Pratt Pond, R — rare (less than 5 collected in all samples), F — frequent (averaged up to 10 in all samples), C — common (averaged more than 10 in all samples), E — epiphyte, T — tychoplankter.

CHLOROPHYTA

Stigeoclonium subsecundum Kuetzing	PP-R-E
Bulbochaete Furberae Collins	IP-C-E
Oedogonium michiganense Tiffany	IP-C-E
O. pseudoplenum Tiffany	IP-C-E
Characium ornithocephalum A. Braun	PP-R-E

Pediastrum Boryanum (Turp.) Meneghini	IP-R-T
P. duplex var. *cohaerens* Bohlin	IP-R-T
P. tetras (Ehrenberg) Ralfs	IP, PP-R-T
P. tetras var. *tetraodon* (Corda) Rabenhorst	IP-C-T
Nephrocytium lunatum W. West	PP-R-T
Kirchneriella contorta (Schmidle) G. M. Smith	PP-R-T
Scenedesmus abundans var. *brevicauda* G. M. Smith	IP-R-T
S. bijuga (Turp.) Lagerheim	IP, PP-C-T
S. dimorphus (Turp.) Lagerheim	IP-R-T
S. quadricauda var. *maxima* West & West	IP, PP-C-T
Actinastrum Hantzschii Lagerheim	IP, PP-C-T
Spirogyra spp.	two easily separable species were common in the vegetative state in Icehouse Pond.
Gonatozygon pilosum Wolle	IP-C-T, PP-R-T
Triploceras gracile Bailey	IP-R-T
Closterium Jenneri Ralfs	IP-R-T
Cl. parvulum Naegeli	IP-R-T
Cl. Ralfsii var. *hybridum* Rabenhorst	IP-F-T
Cl. setaceum Ehrenberg	IP-F-T
Pleurotaenium coronatum (Breb.) Rabenhorst	IP-F-T
P. subcoronulatum var. *detum* West & West	IP-R-T
P. Trabecula (Ehrenb.) Naegeli	IP-C-T
P. Trabecula var. *rectum* (Delp.) W. West	IP-R-T
P. Trochiscum var. *tuberculatum* G. M. Smith	IP-R-T
Euastrum abruptum f. *minor* West & West	PP
E. binale (Turp.) Ehrenberg	IP-R-T
E. ciastonii Raciborski	IP-R-T
E. gemmatum Brebisson	IP-R-T
Micrasterias Nordstedtiana Wolle	IP-R-T

Cosmarium Blytii Wille	IP-R-T
C. difficile var. *dilatatum* Borge	IP-R-T
C. furcatospermum West & West	IP-R-T
C. granatum Brebisson	IP-R-T
C. isthmium W. West	IP-F-T
C. ornatum Ralfs	IP-F-T
C. portianum Archer	IP-F-T
C. pseudoconnatum Nordstedt	IP-F-T
C. pseudopyramidatum Lundell	PP-R-T
C. pyramidatum var. *transitorium* Heimerl	PP-R-T
C. tumidum Lundell	IP-R-T
Staurastrum dejectum Brebisson	IP-F-T
S. gracile var. *nanum* Wille	IP-R-T
S. gracile var. *tenuissima* Ralfs	IP-F-T
S. Leptocladum Nordstedt	IP-R-T
S. Ravenelii var. *spinulosum* Irenee-Marie	IP-R-T
Spondylosium planum (Wolle) West & West	IP-C-T
Desmidium Aptogonum Brebisson	IP-R-T
D. Baileyi (Ralfs) Nordstedt	IP-F-T
Xanthidium cristatum Brebisson	IP-F-T

CHRYSOPHYTA

Tabellaria fenestrata (Lyngb.) Kuetzing	IP-C-T
T. flocculosa (Roth) Kuetzing	IP-C-T
T. quadrisepta Knudson	PP-C-T
Meridion circulare (Grev.) Agardh	IP, PP-C-T
Eunotia elegans Ost.	IP-C-T
E. formica Ehrenberg	IP-F-T
E. pectinalis (O.F.M.) Rabenhorst	PP-F-T
E. pectinalis var. *ventricosa* Grunow	PP-F-T
E. praerupta var. *bidens* (Ehr.) Grunow	IP-F-T
E. tenella (Grun.) Cleve	PP-F-T
E. serra var. *diadema* (Ehrenb.) Patrick	IP-F-T
Hannaea arcus Patrick	PP-R-T
Pinnularia flexuosa Cleve	IP-F-T
P. formica (Ehrenb.) Patrick	IP-R-T
Frustulia rhomboides (Ehrenb.) de Toni	IP-C-T

E. vulgaris Thwaites	IP-F-T
Gomphonema acuminatum var. *coronatum* (Ehrenb.) W. Smith	IP, PP-C-T
G. augur Ehrenberg	PP-C-T
CYANOPHYTA	
Microchaete tenera (Thuret) de Toni	PP-F-T
Hapalosiphon intricatus West & West	IP-C-T
Gloeotrichia Pisum (C. A. Agardh) Thuret	IP-F-E

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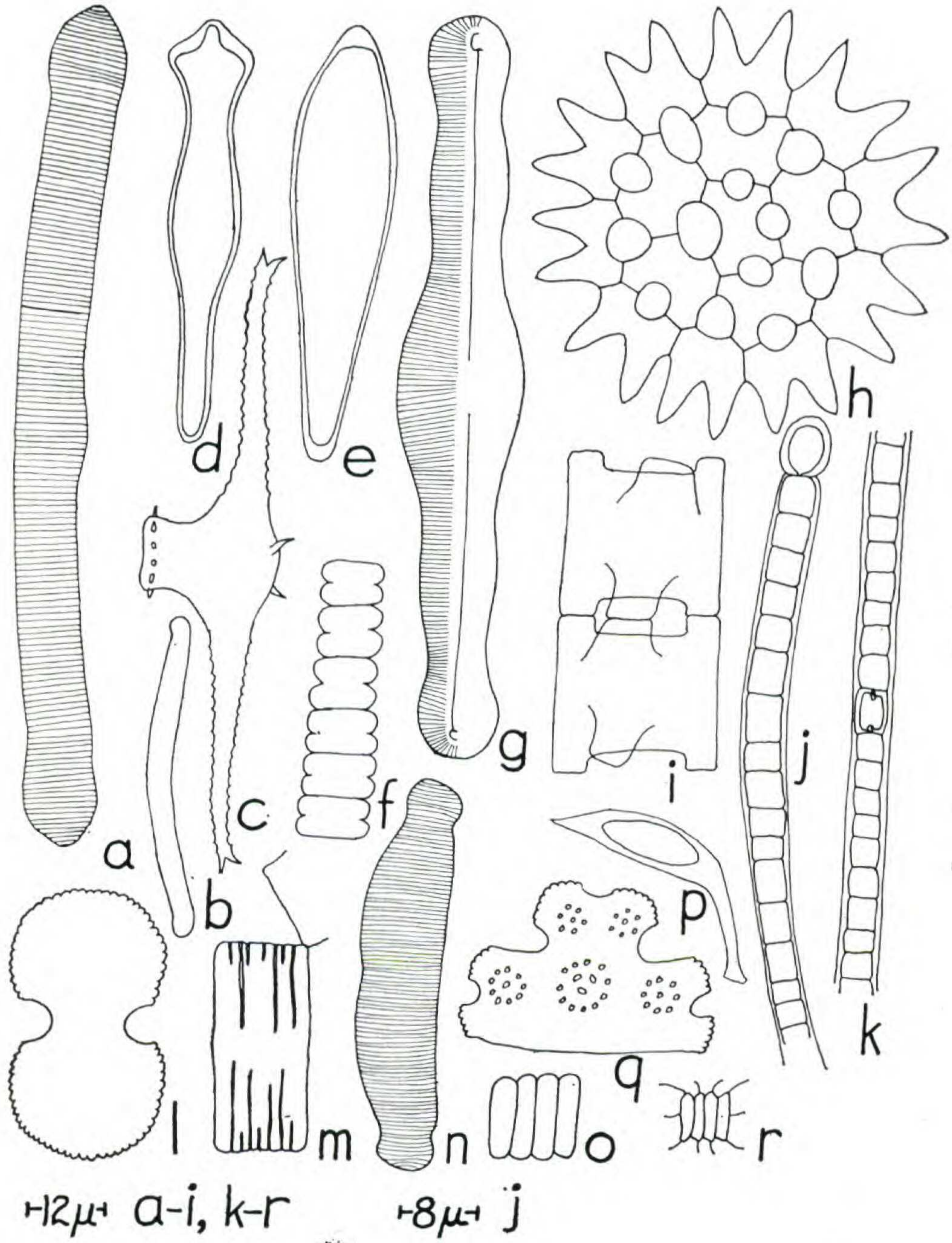

Plate 1

Plate 1:

a) *Eunotia formica* Ehrenberg
b) *E. elegans* Ost.
c) *Staurastrum leptocladum* Nordstedt (semicell)
d) *Gomphonema acuminatum* var. *coronata* (Ehr.) W. Smith
e) *G. auger* Ehrenberg
f) *Spondylosium planum* (Wolle) West & West
g) *Pinnularia formica* (Ehr.) Patrick
h) *Pediastrum duplex* var. *cohaerens* Bohlin
i) *Desmidium Baileyi* (Ralfs) Nordstedt
j) *Gloeotrichia Pisum* (C. A. Agardh) Thuret
k) *Scytonema crispum* (C. A. Agardh) Bornet
l) *Cosmarium isthmium* W. West
m) *Tabellaria flocculosa* (Roth) Kuetzing
n) *Eunotia praerupta* var. *bidens* (Ehr.) Grunow
o) *Scenedesmus bijuga* (Turp.) Lagerheim
p) *Characium ornithocephalum* A. Braun
q) *Euastrum gemmatum* Brebisson (semicell)
r) *Scenedesmus abundans* var. *brevicauda* G. M. Smith

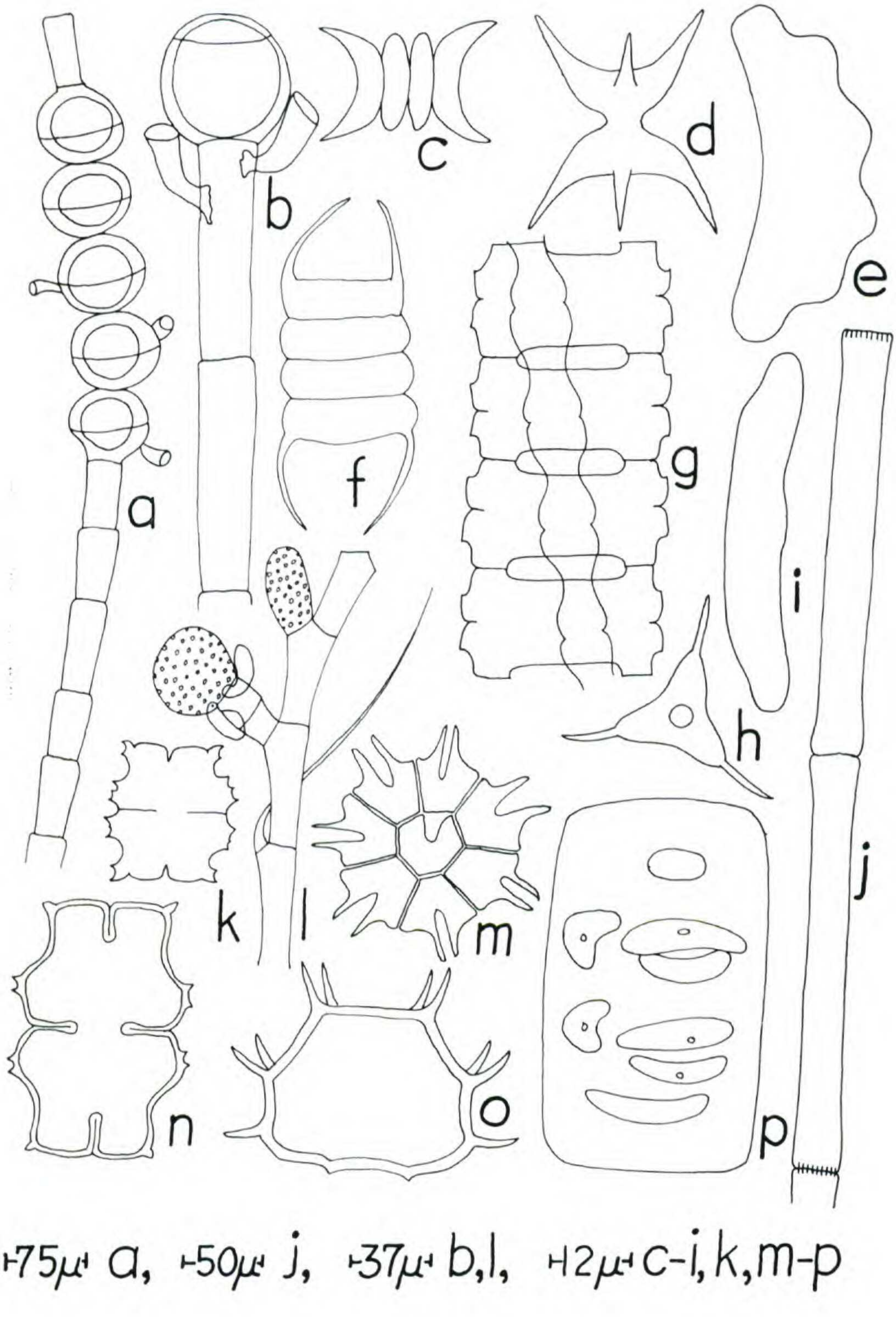

Plate 2

Plate 2:

a) *Oedogonium pseudoplenum* Tiffany
b) *Oe. michiganense* Tiffany
c) *Scenedesmus dimorphus* (Turp.) Kuetzing
d) *Staurastrum dejectum* Brebisson
e) *Eunotia serra* var. *diadema* (Ehr.) Patrick
f) *Scenedesmus quadricauda* var. *maxima* West & West
g) *Desmidium aptogomum* Brebisson
h) *Staurastrum curvatum* var. *elongatum* G. M. Smith
i) *Eunotia pectinalis* (O.F.M.) Rabenhorst
j) *Pleurotaenium subcoronulatum* var. *detum* West & West
k) *Euastrum abruptum* fa. *minor* West & West
l) *Bulbochaete furberae* Collins
m) *Pediastrum tetras* var. *tetraodon* (Corda) Rabenhorst
n) *Euastrum ciastonii* Rabenhorst
o) *Xanthidium cristatum* Brebisson (semicell)
p) *Nephrocytium lunatum* W. West